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Investigations on the sciurid manus

II. Analysis of functional complexes by morphological integration and by coefficients of belonging

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Introduction

Functional complexes were studied by correlations in the bones of the manus of three different squirrels and compared with those of aerial bats. The analysis of correlation matrices was accomplished two ways, by using measures of morphological integration (OLSON and MILLER 1958; see VAN VALEN 1965) and also, for the first time in biology, a relatively simple factor analytical method using "coefficients of belonging" (HARMAN 1967). Patterns of variation were observed, and the studies on correlation were performed to relate structure of the sciurid forefoot with its functions.

Methods

The bones of the right forelimbs of Wisconsin adult *Glaucomys volans* (30) and of the manus in *Spermophilus tridecemlineatus* (20) and *Sciurus carolinensis* (20) were boiled at low temperature in ammonia hydroxide and cleaned. The small bones were measured in microns by means of a Gaertner Slide Micrometer. Dial calipers accurate to 0.02 hundreths of a millimeter were used for the radius and humerus. The *Spermophilus* and *Glaucomys* were difficult to clean, until the partially cleaned bones were softened and cleared in petri dishes containing glycerin. All measurements were made at 20 °C, and each bone was measured three times.

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Table 1

Coefficients of variation (± SE) for the bones of the manus in three squirrels and one bat

	MET. V	V, 1	V, 2	IV	IV, 1	IV, 2	III	III, 1	III, 2	II	II, 1	II, 2	Means
Spermophilus (semi-fossorial)	5.03 ± .82	4.51 ± .73	7.92 ± 1.3	4.03 ± .65	4.83 ± .78	6.03 ± .98	4.02 ± .65	4.60 ± .75	5.22 ± .85	4.39 ± .71	4.91 ± .80	6.16 ± 1.0	5.14
Sciurus (scampering-arboreal)	4.91 ± .80	3.84 ± .62	4.44 ± .72	4.18 ± .68	3.60 ± .58	4.13 ± .67	4.42 ± .72	3.37 ± .55	3.82 ± .62	4.81 ± .78	3.62 ± .59	5.09 ± .83	4.18
Glaucomys (arboreal-volant)	3.94 ± .52	3.55 ± .47	4.00 ± .52	3.65 ± .48	2.40 ± .31	3.66 ± .48	3.93 ± .52	2.51 ± .33	3.39 ± .44	4.20 ± .55	3.17 ± .42	6.80 ± .89	3.77
Tadarida (aerial)	2.95 ± .30	3.47 ± .38	10.75 ± 1.2	—	—	—	2.59 ± .26	3.45 ± .36	4.78 ± .50	2.78 ± .30	18.47 ± 2.0	—	—

Results

Variation patterns

The coefficient of variation (CV) determined for the bones in the manus of *Spermophilus*, a semi-fossorial form; *Sciurus*, arboreal; and *Glaucomys*, a volant squirrel are compared with those previously reported for the aerial bat *Tadarida* in Table 1 (Bader and Hall 1960; Long and Kamensky 1967). The marked trend reported in bats, namely increased variations distally, is not seen in these squirrels. The reasonable explanation for this may be that the distal phalanges are clawed and functional in squirrels, but vestigial or lost generally in bats (except the thumb which expresses low variation).

Volant *Glaucomys* resembles bats somewhat in variation as well as in function showing interesting high variation distally in digit II. Variation of the second phalanx is nearly double the mean CV (3.77). In *Tadarida* the second phalanx has been lost, and the now vestigial and distal first one had a remarkably high CV of 18.47, almost identical with the values found in two *Myotis* bats (Bader and Hall 1960). The ground squirrel *Spermophilus* showed an apparent upswing in CV values in the second digit, but the second phalanx, which has a far different function than in volant-arboreal *Glaucomys* (CV: 6.16) was not much more variable than average (mean CV: 5.14).

The mean CV's decreased from the semi-fossorial *Spermophilus* to arboreal *Sciurus* (4.18), and to volant *Glaucomys* (3.77). *Sciurus* showed little fluctuation in variation in the forelimb.

Exceptionally low variations were evident in the first phalanges of the third and fourth digits in *Glaucomys*, and these same bones were relatively low in *Sciurus* and *Spermophilus*. In the two scansorial squirrels the pattern was consistently low in variations of the first phalanges, whereas in bats and Spermophilus the metacarpals were low.

High CV's included the second phalanges of digits V, IV, and II in *Spermophilus*, and probably II, phalanx 2 in *Sciurus* and especially in *Glaucomys*.

The volant *Glaucomys* might be expected to approach the aerial pattern of birds and bats (Bader and Hall 1960; Long and Kamensky 1967), but two very different evolutionary phenomena are probably involved. Savile (1957) suggested and most workers accept that primitive birds were soarers with long wings evolved, that subsequently shortened. Modern bats are likewise in the process of shortening their wings, having lost some of their distal phalanges. On the other hand, *Glaucomys* has not attained soaring wings and is apparently in the process of elongating the bones in the forelimb (see Piterka 1936). Nevertheless, in the low variation (high function) of the outer digits and high variation (low function) of the distal elements of digit two the volant and aerial forms resemble one another and differ greatly from the pattern of variation and function (Long and Captain 1974) of semi-fossorial *Spermophilus*.

Correlation and morphological integration

The Pearson correlation coefficient (r), converted to Z, was used to measure the association of bones in the manus in *Sciurus*, *Glaucomys*, and *Spermophilus*. The samples were not as large as desirable, but the conclusions obtained, by two different methods, seem conservative and reasonable in regard to function and form. Functional complexes can be identified by correlation (Olson and Miller 1958; Van Valen 1965), and in our study the levels of significance were used to reveal factors of morphological integration. The results (see Figure) of squirrels varying from terrestrial to volant adaptive zones were compared to findings on the only aerial mammals, the bats (Long and Kamensky 1967; Bader and Hall 1960, although in the latter only significant r's were published).

Serial homologues, defined as bones of the digits occupying the same position (e. g., metacarpals of digits III and IV), showed the highest correlations. In tables 2, 3, 4, the serial bones are readily studied by reading in the diagonals arising from

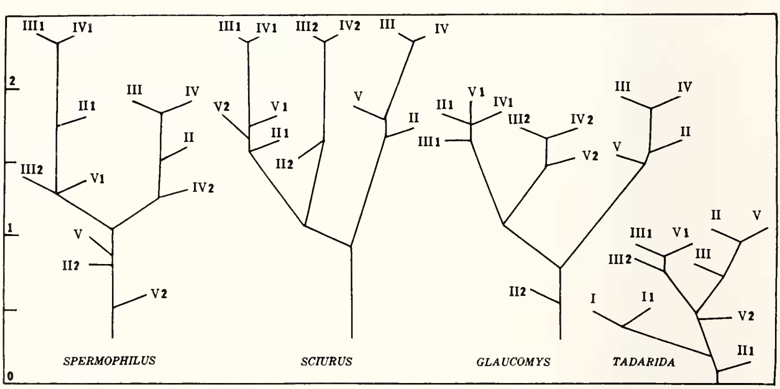

Fig. Dendrograms for *Spermophilus*, *Sciurus*, *Glaucomys*, and *Tadarida* showing levels of morphological integration by means of Z values. Roman numerals refer to metacarpals, Arabic numerals to phalanges. The bones of the pollex and in *Tadarida* digit IV were omitted. Concerning *Spermophilus*, other reasonable interpretations associate V, p. 1 and V as a separate group, or II, 2 and III, 2 as separate and having affinity with IV, 2; II; III; and IV.

Table 2

Correlation coefficients of bones of the manus in *Spermophilus*

The values for serial homologues in the lower, left diagonals are coefficients of determination (r^2). N, 19. Second phalanges show low r^2 values. Metacarpal shows alienation to other metacarpals particularly with III

Bone	II, met.	II, p. 1	II, p. 2	III	III, p. 1	III, p. 2	IV	IV, p. 1	IV, p. 2	V	V, p. 1	V, p. 2	$\sum r$
II		.84	.72	.87	.76	.83	.93	.77	.88	.75	.78	.54	8.67
II, p. 1			.57	.81	.93	.84	.80	.95	.80	.62	.89	.45	8.50
II, p. 2				.65	.57	.82	.71	.56	.78	.67	.37	.50	6.92
III	.76				.71	.78	.95	.69	.79	.56	.66	.40	7.92
III, p. 1		.86				.87	.76	.98	.71	.62	.79	.30	8.05
III, p. 2			.67				.79	.87	.82	.59	.71	.41	8.43
IV	.86			.90				.75	.83	.78	.74	.48	8.52
IV, p. 1		.90			.96				.72	.60	.83	.34	8.06
IV, p. 2			.61			.67				.72	.72	.62	8.39
V	.56			.31			.61				.78	.36	7.05
V, p. 1		.79			.62			.69				.46	7.73
V, p. 2			.25			.50			.38				4.86

Table 3

Correlation coefficients of bones of the manus in *Sciurus*

The values for serial homologues in the lower, left diagonals are coefficients of determination (r^2). N, 19. All bones, even the second phalanges, show high r^2 values

Bone	II, met.	II, p. 1	II, p. 2	III	III, p. 1	III, p. 2	IV	IV, p. 1	IV, p. 2	V	V, p. 1	V, p. 2	$\sum r$
II		.75	.59	.95	.76	.60	.88	.70	.51	.93	.73	.67	8.07
II, p. 1			.71	.83	.93	.72	.83	.89	.80	.84	.92	.92	9.14
II, p. 2				.73	.78	.95	.79	.79	.89	.65	.66	.86	8.40
III	.90				.83	.72	.98	.77	.63	.95	.77	.73	8.89
III, p. 1		.86				.82	.87	.98	.86	.83	.94	.91	9.51
III, p. 2			.90				.81	.85	.98	.69	.74	.92	8.80
IV	.77			.96				.84	.70	.93	.79	.77	9.19
IV, p. 1		.79			.96				.90	.79	.94	.92	9.37
IV, p. 2			.79			.96				.53	.81	.89	8.50
V	.86			.90			.86				.83	.78	8.75
V, p. 1		.85			.88			.88				.94	9.07
V, p. 2			74.			.85			.79				9.31

metacarpals III, IV, and V. In *Sciurus* the r's in the first diagonal exceed 0.90 except one between phalanx 2 of digits IV and V (which is 0.89). In *Spermophilus* and *Glaucomys* the serial bones correlate strongly also, with some interesting exceptions (see below). In bats *(Myotis)* the serial bones showed high correlation according to Bader and Hall (1960). Adjacent bones in a digit usually showed higher correlation than separated bones.

Table 4

Correlation coefficients of bones of the manus in *Glaucomys*

The values for serial homologues in the lower, left diagonals are coefficients of determination (r^2). N, 29. Some of the second phalanges show low r^2 values

Bone	II, met.	II, p. 1	II, p. 2	III	III, p. 1	III, p. 2	IV	IV, p. 1	IV, p. 2	V	V, p. 1	V, p. 2	Σ r
II		.68	.34	.93	.66	.46	.88	.69	.45	.90	.70	.41	7.10
II, p. 1			.58	.64	.92	.72	.58	.91	.70	.68	.94	.78	8.13
II, p. 2				.37	.53	.61	.32	.55	.62	.34	.58	.74	5.58
III	.86				.62	.39	.95	.64	.41	.92	.66	.38	6.91
III, p. 1		.85				.75	.59	.92	.74	.58	.93	.80	8.04
III, p. 2			.37				.32	.77	.93	.32	.78	.86	6.91
IV	.77			.90				.58	.38	.88	.64	.36	6.48
IV, p. 1		.83			.85				.73	.59	.94	.76	8.08
IV, p. 2			.38			.86				.30	.81	.92	6.99
V	.81			.85			.77				.70	.34	6.55
V, p. 1		.88			.86			.88				.83	8.02
V, p. 2			.55			.74			.85				7.18

Table 5

Relation between high variation and low correlation

	High					Lower			
	Bone	CV	Mean r	Mean k		Mean k	Mean r	CV	Bone
Tadarida	II, p. 1	18.47	.12	.99	>	.92	.39	3.45	III, p. 1
Spermophilus	V, p. 2	7.92	.44	.90	>	.66	.75	4.02	III, p. 2
Glaucomys	II, p. 2	6.80	.51	.86	>	.77	.64	3.66	IV, p. 2

In *Spermophilus* the bones of the fifth digit hardly correlated with their serial homologues, probably because V is becoming vestigial. Phalanx 2 of digit II showed somewhat low correlation with other bones (except in *Sciurus*) possibly because this phalanx is somewhat high in variation (see above).

An inverse relation between high variations and low correlation is shown in table 5. Where the statistic k is the coefficient of alienation (the square root of $1 - r^2$). These results are not surprising for the Pearson correlation coefficient measures proportionate deviations in common, and if one bone becomes variable the proportions are altered. High variation or low correlation shows a low degree of functional use.

The coefficient of determination (r^2) shows what per cent of the variability of one variable is explained by variability af another. These coefficient are listed for the serial homologues in the correlation tables 2, 3 and 4 in the lower left diagonals. In many instances these values exceed 80 per cent, reflecting the strong developmental homeostasis expected of serial homologues. Low values (alienation) apparently resulted from a changed function of a digit, especially in digit V of *Spermophilus*.

In *Sciurus* the second phalanx of digit V showed high correlation with more bones than did the other second phalanges; V, p. 2 showed high correlation with II, p. 1; III, p. 1; IV, p. 1; and V, p. 1. This may be a result of elongation and functional importance of V, p. 2 in a scansorial squirrel (LONG and CAPTAIN 1974).

In *Spermophilus* the only exceptional characteristic noted was the relatively low correlation of the distal serial homologues. The highest r observed was of III, p. 1 and IV, p. 1. Surprisingly, IV, p. 2 fit with several metacarpals (Fig. 1). In *Glaucomys,* II, p. 2 stands alone, but basically the pattern of Z correlation closely resembles that of *Sciurus* (Fig. 1).

Coefficients of belonging

Another method of analyzing correlation tables and of verifying findings of morphological integration is the grouping of variables on the basis of their intercorrelations by means of coefficients of belonging (B-coefficients). B is defined as 100 times the ratio of the average of the intercorrelations among the variables of a group to their average correlation with all remaining variables (HARMAN 1967). Variables that show notable intercorrelation are grouped by the equation,

$$B_j = 200\ (n-v)\ S/(v-1)\ T$$

where n is the total number of variables (kinds of bones in this case), v is the number of correlations assigned tentatively to a group (for example, between metacarpals II and III, II and IV etc.), S is the summation of intercorrelations of these variables, and T is the sum of their correlations with the remaining variables. T is calculated by $T = \Sigma r_{e_1} + \Sigma r_{e_2} - 2r_{e_1e_2}$ when $r_{e_1e_2}$ has the highest correlation, and subsequently by a recurrence formula $T_v = T_{v-1} + \Sigma r_{eb} - 2L_v$, where b is the last variable added (because of a high r) to the group, and L is Σr_{bj}. The last summation is the sum of correlations of b and j variables in the group. S_v is the sum of S_{v-1} and L_v. A precipitous drop in the B-coefficient causes removal of the last variable from the group. Clear examples are provided by HARMAN (1967).

By means of B-coefficients the group factors of the correlation table for *Sciurus* and *Glaucomys* revealed only the importance of serial homology. The metacarpals constituted a distinct group, and the first and second phalanges together made up a second group. In both of these scansorial squirrels the last variable added was the second phalanx of digit II. The groupings were remarkably similar, and resembled somewhat those of the bat *Tadarida,* in which the vestigial index phalanx (II, p. 1) was itself a separate group (see below). The B-coefficients of *Sciurus* were markedly lower than in *Glaucomys* because of a high overall correlation in the former, perhaps related to its greater problem (for climbing) of weight (*Sciurus* B: 115–127; *Glaucomys* B: 132–181).

In *Spermophilus* there were two notable exceptions to groupings resulting from serial homology. Phalanx two of digit three fit in the grouping of first phalanges. In *Spermophilus* there was difficultiy in assigning metacarpal V to the metacarpal group, but V fit with IV, p. 2 and II, p. 2. The phalanx V, p. 2 stood alone. Probably the peculiarity of digit V results from its shortening and loss of function (LONG and CAPTAIN 1974). The groups were as follows: 1. phalanges III, p. 1; IV, p. 1; II, p. 1; III, p. 2; and V, p. 1; 2. metacarpals III, IV and II; 3. IV, p. 2; II, p. 2; and V; and 4. only V, p. 2.

The use of B-coefficients for the r-table recorded by LONG and KAMENSKY (1967) for the free-tailed bat, *Tadarida brasiliensis,* revealed that the correlation of serial homologues was obscured by the distinct groupings of 1. nearly all bones in the wing; 2. metacarpals I and I, p. 1; and 3. finally II, p. 1, which stood alone. The loss of function and/or high variation in vestigial II, p. 1 and the different function of clawed digit I from the other bones in the wing doubtless account for these three groupings.

The B-coefficient varies as a result of a change in the numerator (intercorrelation) or denominator (out-group correlation). A high r important in morphological integration may fail to live up to its promise if other correlations are low. The loss of variables from the denominator, when V is high, may lead to fluctuation of the value of B. B-coefficients provide confidence from verification by a different analysis of an r-table and bring to light the importance of some groupings perhaps not noticed in other tests. They provide a conservative, reasonable analysis of a correlation table, as can be seen by the close correspondence of coefficients of *Glaucomys* and *Sciurus* which are fairly close in relationship (Long and Captain 1974; Black 1963).

Acknowledgements

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Summary

Patterns of variation and correlation of the bones of the forelimb were observed in semi-fossorial, arboreal, and volant squirrels and compared to those in aerial bats. Sciurids did not resemble bats in high variations of distal bones, but serial homology was an important reason for high correlations in all these mammals. In volant *Glaucomys*, as in the aerial bats, the distal phalanx of the index digit showed high variation and low correlation. From the semi-fossorial, arboreal, volant, to aerial mammals studied, the bones in the forelimb showed a general trend in reduced variation (excluding vestigial bones). Coefficients of determination were high (often exceeding 80 per cent) in serial homologues in the sciurid manus, but were low for digit V of the semi-fossorial *Spermophilus*. Digit V in *Sciurus* and *Glaucomys* shows functional importance. Patterns of correlation in *Sciurus* and volant-arboreal *Glaucomys* are similar. The methods for identifying functional groupings by morphological integration and by a simple kind of factor analysis involving "coefficients of belonging" yield similar results. Biologists should consider the application of either or both techniques to problems on correlations. Coefficients of belonging are easily calculated.

Zusammenfassung

Untersuchungen an der Hand von Sciuriden. II. Analyse der Längen von Phalangen und Metacarpalia bezüglich ihrer Variabilität und Interkorrelationen

An je einer Serie von grabenden *(Spermophilus tridecemlineatus)*, baumlebenden *(Sciurus carolinensis)* und gleitenden *(Glaucomys volans)* Sciuriden wurden die Längen der Metacarpalia und Phalangen gemessen, ihre Variationskoeffizienten (Tab. 1) und die Korrelationskoeffizienten zwischen allen Elementen derselben Art (Tab. 2—4) berechnet. Die distalen Phalangen variieren weit weniger als bei einer Fledermaus *(Tadarida)*. Relativ hoch ist nur die Variabilität der 2. Phalange des 2. Fingers beim Flughörnchen *(Glaucomys)*. Die mittlere Variabilität der Handknochen nimmt von *Spermophilus* über *Sciurus* zu *Glaucomys* ab. Die Korrelationskoeffizienten zwischen Knochen einer Serie (etwa zwischen verschiedenen Metacarpalia) sind im allgemeinen höher als zwischen nicht Serienhomologen (etwa zwischen irgendeinem Metacarpale und einer ersten Phalange). Nur schwach korreliert mit homologen Elementen der übrigen Strahlen sind die des 5. Fingers von *Spermophilus*. Das mag mit seiner relativen Bedeutungslosigkeit zusammenhängen. Zur Feststellung, welche Knochengruppen enger korrelieren, eignet sich der „Zusammengehörigkeits-Koeffizient" (coefficient of belonging) nach Harman (1967). Seine Berechnung bestätigt die schon aus der Betrachtung der Korrelationskoeffizienten ermittelten Gruppierungen, kann aber weitere, zunächst übersehene Zusammengehörigkeiten aufdecken.

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Reproduction of the multimammate rat, *Praomys (Mastomys) natalensis* (Smith), in Uganda

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Introduction

Multimammate rats are common throughout Africa south of the Sahara. They usually live in savanna, cultivated land, or around human habitation. Their growth and breeding biology has been studied in many areas because they are important carriers of human plague and they may also be serious agricultural pests (KINGDON 1974).

The specific validity of the various described forms is open to question. Chromosome studies have revealed that the form *natalensis* (Smith) from South Africa has 36 chromosomes, the West African form *erythroleucus* (Temminck) has 38 chromosomes, and another unnamed form from West Africa has 32 chromosomes (MATTHEY 1966, 1973). The relationship of Uganda *Mastomys* to these species is not known. They are provisionally referred to the form *natalensis* (DELANY 1975), but chromosome studies are required to help determine their status in relation to the South and West African forms.

Studies by BRAMBELL and DAVIS (1941) in Sierra Leone, CHAPMAN et al. (1959) in Tanzania, DIETERLEN (1967) and PIRLOT (1954) in Zaire, SHEPPE (1972, 1973) in

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